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On the optics of the dolphin eye

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Introduction: a long history and its results

It goes without saying that great differences exist between water and land as an environment for life. Animals have to be adapted to the mechanical, chemical, osmotic and other conditions that prevail in the medium in which they live. To the eye, an optical organ, the very different optical conditions in water and in air have been decisive in its design, resulting in two optically different types: the aquatic and the aerial eye.

The eye originated in water; with regard to vertebrates, already in the earliest times fish existed with well developed eyes. These eyes were passed via amphibians and reptiles to birds and mammals, meanwhile being greatly modified, in the first place to enable it to survive in dry air and, in addition, to keep it functioning satisfactorily. We all bear witness that this experiment succeeded reasonably. But the experiment continued: representatives from the various vertebrate classes returned to the water, necessitating new adaptations. Several mammals went this way, the whales and dolphins so far that their eyes became very fishlike (Fig. 1). There are some important differences, however, functional and anatomical. With respect to the first, we know from experience with dolphins in captivity and also from the work of Herman c.s. (1975) that these animals can see well in water and, very un-fishlike, also in air. Secondly, whereas in the typical fish eye the pupil has an approximately round outline, and is hardly or not at all contractile, in dolphins we are confronted with a most peculiar pupillary shape and mobility (Fig. 2). If fully opened, the pupil has the 'regular' shape of a horizontal oval. In closing, however, its upper edge is lowered down, forming a so-called operculum, which descends until a narrow U-shaped slit, or only two tiny vertical slits remain. It is clear that if an animal has such an apparently special device, it must also serve a special task. This task and the dolphin's capability of amphibious vision may well be connected. In trying to explain the possible connection it is necessary to go into some principles of light refraction by lenses. After such an exercise also another aspect of dolphin vision—which finds its expression in the retinal structure—is more easily understood. Therefore we will also shortly discuss that aspect in this paper.

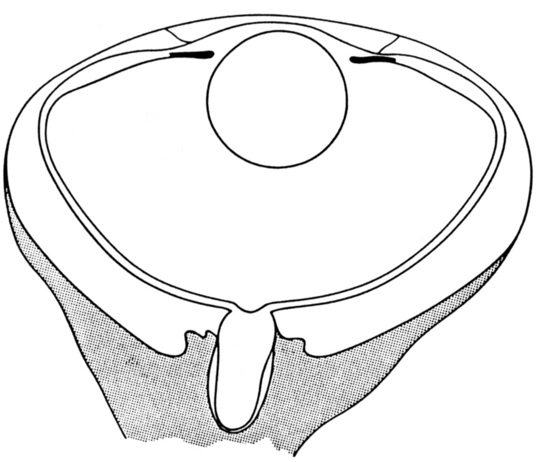

Figure 1. Schematic horizontal section through the eye of a dolphin. From Dral, 1985.

Aerial and aquatic vision

It may be convenient to start our expositions with a look at the human eye. Light entering this eye, as indicated by the broken lines in Fig. 3, is first refracted by the cornea, passes the pupil, is refracted again at the front surface of the lens and thirdly at its rear surface, to finally form an image point on the retina. Most of the refraction, about 60%, is performed by the cornea, so that the light is already considerably converged when it reaches the lens, in which way the eye is provided with a wide field of vision.

If we put this eye under water, refraction by the cornea is diminished to practically zero because of

Figure 2. Shapes of the dolphin's pupil in various stages of contraction. From Dral, 1985.

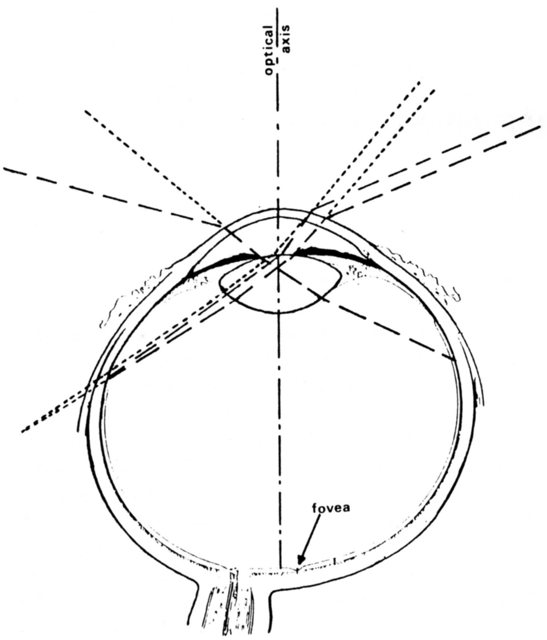

Figure 3. Scheme of a section through the human eye. The paths are traced of light rays entering the eye from air (broken lines) and water (dashed lines).

the near parallelism of its surfaces and the close similarity of the refractive indices of the aqueous humor at the inner side and the water which is now at its outer side. The result is that the image point shifts to a location far behind the retina (the dotted lines in Fig. 3). In other words: the eye becomes strongly far-sighted. Moreover, the field of view is considerably narrowed. These are some of the problems the predecessors of the dolphins met when they decided to exchange their terrestrial way of life for an aquatic one.

The adaptations which took place in the dolphin's eye to remove these disastrous effects become clear in comparing Fig. 1 with Fig. 3. To widen the field of vision again, the only remaining refractive device, the lens, was shifted forward, much in the fashion as in fish. Secondly, to compensate for the loss of refraction by the cornea, the lens became more strongly curved and, in addition, its material became more highly refractive, both factors again much as in fish. By these measures the eye is rendered right-sighted under water. The shape of the lens and its location characterize the dolphin eye as a basically aquatic one, just as is found in aquatic animals like fish.

The problem of amphibious vision

Thus, the dolphin's eye is well adapted to underwater vision. But, as we know, dolphins see equally well with their heads out of water, despite the fact that in

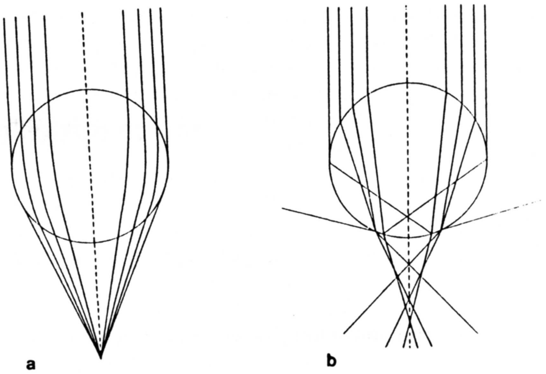

Figure 4. Refraction of light in (a) a fish eye lens and (b) a homogeneous glass sphere. After Pumphrey, 1961, modified.

air refraction by the cornea inevitably comes in addition, which would make the eye strongly near-sighted in these circumstances. This clearly not being the case, we must look for a mechanism to compensate for the added corneal refraction. The trick to perform aquatic as well as aerial vision is mastered by quite some amphibious living species (although not in amphibians!), like the seals, the otter, diving birds and reptiles (Sivak, 1978). These animals, however, have basically aerial eyes, for which the problem is the other way around. They have to *gain* refractive power when they dip their heads under water; the dolphin requires *loss* of refractive power when it raises its head in air. No accommodative mechanism is known to perform the latter. So the mechanisms used by the species mentioned above cannot be applied by the dolphin. There exist some other aquatic eyes with an amphibious function, like those of flying fishes and of the four-eyed fish (Sivak, 1978), but the mechanisms found in these species are not present in dolphins. So, in the case of the dolphin we have to look for something original, something that as far as we know has been realized nowhere else. As yet we know nothing for sure about this matter, but there is a theory which has the advantage that it neatly fits all observations done on this subject. It is in this theory, proposed by Rivamonte (1976), that the peculiar shape of the pupil receives a function.

Spherical aberration and its correction

Before we can explain the principles of Rivamonte's theory we have to know something more about refraction by lenses. Any lens has a front and a rear surface of which at least one is curved and, as a rule, is curved spherically. Such a lens has the property to deviate light passing through its marginal parts more strongly than light passing through its central part, and increasingly so from the centre outwards. This so-called spherical aberration is tremendous in a homogeneous globular lens (Fig. 4b). As a result such a lens has not even a defined focal point; the place which comes nearest to a focal point is reached by only a small percentage of the light. Natural lenses, however, are not made out of homogeneous material, like a glass sphere is; instead they have a high refractive index at the core, gradually (or maybe stepwise in concentric shells) decreasing towards the periphery (Fig. 4a). Thus the spherical aberration is eliminated. This is the case in all vertebrate eye lenses (a contribution to the correction can also be achieved by an alteration of the shape of the refracting surfaces). As is known from measurements on the globular lenses of fishes, the correction is complete and leads to a perfect focal point (e.g. Fernald and Wright, 1983).

Rivamonte's theory

The same must be the case in dolphins, though, according to Rivamonte's theory, in their lenses the correction would be exaggerated. The dolphin eye lens would be spherically overcorrected, which means that the lens is supposed to have a shorter focal length for light passing through the core than for marginally passing light rays. Let us, with this in mind, again look at the dolphin eye with its peculiar pupil. When the pupil is opened, in conditions of low light intensities which will prevail under water, the whole lens is exposed to the entering light. Most of it passes through the core of the lens, being maximally refracted and producing a well focused image on most of the retina. This image would be superimposed by a far-sighted image, formed by the smaller amount of light passing through the margin of the lens. The result would be a well focused image with the quality which is known as 'soft focus' in photography. With the eye in air and exposed to more light, the pupil will assume a horse-shoe shape. The operculum obscures the core of the lens, while the remaining slit leaves a passway to the light mainly through the margin of the lens. Because of the spherical overcorrection the light would be less refracted there, but addition of the refraction by the cornea again would result in a well focused image on the retina. On part of this image a near-sighted image may be super-imposed, formed by some light passing through the lens core and again leading to a 'soft focus' effect. In both media the image would be well focused, the 'soft focus' impairing the contrasts somewhat. Thus Rivamonte's theory explains the dolphin's ability to see well both in water and in air. A more detailed description is found in Rivamonte's original paper (1976) and in Dral (1985).

The blessings of a spherical lens

It should be realized that images, formed by lenses, are not projected on a flat surface, as is the case in a photographic camera (and to which end the photographic lens is specially designed), but, instead, are formed on a spherical surface. This is quite easily understood by another look at Fig. 4a. In this figure the light comes vertically from above but, due to the symmetrical shape of the (spherical) lens, it would make no difference if the light came from any other direction; the picture would always show the same courses of the light rays. If the light source would make an excursion from left to right, the focal point obviously would travel along a circular path from right to left. Or, in other words, a plane object would be imaged on a spherically curved surface. This so-called Petzval curvature of the image may well be the reason why the retina of the vertebrate eye is spherically shaped.

Though such curvature is inherent to all images formed by lenses, the ideal conditions as sketched above only hold for a spherical lens, being well corrected for spherical aberration. Lenses of a more flattened shape (or systems of lenses) as is the case in the human eye (Fig. 3), have an optical axis, represented by a line passing through the lens centre and the apices of its curved surfaces. It is along this line and a very narrow area around it that the image has the highest quality. The image formed by light passing through the lens at more oblique angles is impaired by a defect called oblique astigmatism which means that of an object point two separate line foci are formed. It is partly for this reason that in our eye one relatively tiny spot exists where we see perfectly well, namely at the fovea in the centre of the yellow spot. Another reason is that more than in agreement with the deterioration of the image, the retina becomes peripherally increasingly less capable of good resolution. For these reasons we have to move our eyes in order to read a line. Of course the eye has made the best of it and so we find that peripherally the retina is located between the two images (the 'tangential' and 'sagittal' one in Fig. 5) which results from oblique astigmatism.

With regard to the dolphin eye, the above mental experiment with the moving light source also clarifies that the symmetrical lens has an infinite number of optical axes and thus is free of oblique astigmatism. There is no reason why the image on a certain place of the retina would be of lesser or better quality than anywhere else. In accordance we do not find one tiny spot of maximum resolution, as in the human eye, but an extended field of equally good resolution with two large areas of maximum resolution, one for vision sidewards and another for vision, binocularly, straight ahead (Fig. 6). A pattern reminiscent to this has been found in some lower vertebrates; among mammals, the dolphins are unique.

Because the dolphin eye under water is not subject to oblique astigmatism, one may expect that the image, and hence the retina, will coincide with the

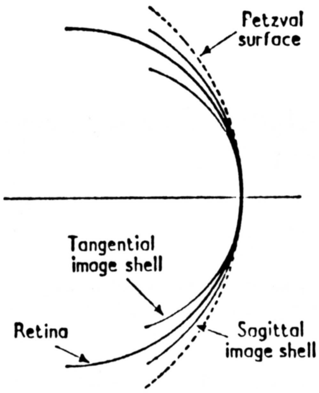

Figure 5. The position of the image shells, the retina and the Petzval surface in the human eye. From Bennett and Francis, 1962.

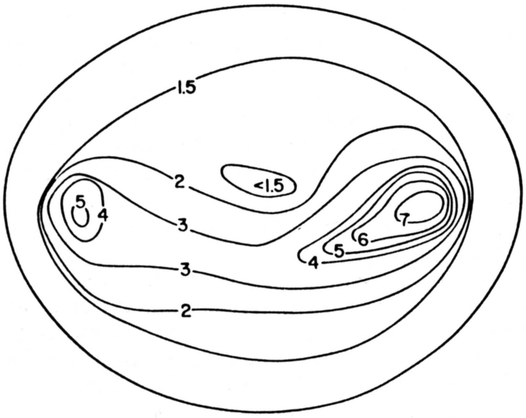

Figure 6. Flat projection of the retina of the right eye of a *Delphinus delphis*. Shown are the numbers (in hundreds) of ganglion cells per mm^2, which gave an indication for the regional resolution capacity of the retina. From Dral, 1983.

Petzval surface. If we calculate the radius of the latter with the data presented in Rivamonte's eye model, it appears that with the eye in water such a coincidence indeed exists. If the eye is raised in air, however, the addition of the refracting cornea renders the eye into an optical system with one unique optical axis, inevitably entailing oblique astigmatism. If we calculate the Petzval curvature in these circumstances, it appears to be a bit shallower, as it is in the human eye (Fig. 5) and probably with the same effect: the retina remains at the position where the image quality is at best.

The necessity to compromise

In regarding an eye like that of the dolphin with its—at least under water—perfect image all over the field of vision, one might wonder why that image is not completely resolved by the whole retina. Instead that, this is the only case, more or less, at the two areas (Fig. 6); a large part of the visual field is confined to a less detailed resolution. The same question might be asked with regard to the human eye, where outside the fovea the retinal resolution is less than would be allowed by the image quality. In both cases the answer may be related to the necessity to economize on the neural part of the visual process. Detailed information from larger parts of the retina would require a great number of axons for transfer to the brain. This might enlarge the blind spot to unacceptable proportions, while the brain, where that information has to be processed, has its limits too. We can convince ourselves that in the case of human vision, after its long history of adaptation, the eventual compromise between desirabilities and possibilities yields exactly the capacity that we require. In this sense our eye is perfect. We may keep ourselves convinced that to the dolphin its eye is of equal perfection.

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